PHYLLOSPADIX AS A BEACH-BUILDER.[1]

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In December, 1898, while overhauling a heap of seaweeds recently collected by Prof. W. A. Setchell and myself at Bodega Bay, California, I discovered, clinging to a branch of Amphiroa, a small brown object which bore, at first sight, a rude resemblance to a beetle's head with rigid, bristle-fringed antennæ. On examination, however, it was evident that this nondescript, clasping the Amphiroa in such a way that the reflexed bristles, or "barbs," of its arms resisted attempts to detach it, was the seed or fruit of some flowering plant. Further, it was obvious that this contrivance of arms and bristles was a unique and most interesting example of dissemination mechanism.

As there are extensive beds of eelgrass (Phyllospadix) growing in shallow water along the rocky shores of Bodega Bay, the possibility suggested itself that this was the ripe fruit of Phyllospadix, and upon comparison with the figures of Ruprecht and others it seemed that such was the case,— although our find was, in some respects, very different from what Ruprecht supposed to be the "ripe fruit."[2]

A few weeks later, at Monterey Bay, the matter was put beyond doubt, and given new complexity and interest, when we collected not only an abundance of the fruits, but also young plants in several stages of development. Following up these discoveries, and with the help of Professor Setchell and Dr. W. L. Jepson, I made an investigation, the results of which are here set forth. These results, to anticipate a summary, are, first, some data as to the life history of Phyllospadix, and, second, some speculation as to the significance of the plant from a geological point of view.

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[1] Thesis for the degree of M.S., University of California, May, 1900.

[2] Ruprecht, F. J. Neue . . . Pflanzen aus dem . . . Stillen Oceans. 1852.

First we consider the fruit itself. Upon comparison of Figs. 2 and 3 it is seen that our wave-beaten specimen from Bodega, with its long stiff arms, lined with brushes of inflexed bristles, is a decided departure from Fig. 2, which represents the most mature fruit I have been able to find still attached to the spadix. Fig. 2 is also an approximate reproduction of Ruprecht's figure. Fig. 1 shows a younger stage.

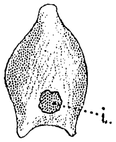

FIG. 1.

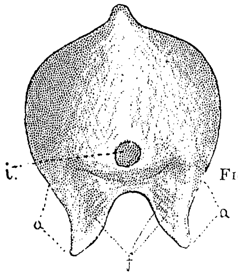

FIG. 2.

FIG. 1.—Early stage of fruit.

FIG. 2.—Later stage of same.

The feature which catches the attention in Fig. 3 is, of course, the arrangements of the two arms, with the bristles or barbs. This is what I have called the "dissemination mechanism"; but that is rather a misnomer, for it is a device, not for scattering the seeds, but for anchoring them after they have been drifted away from the parent plant.

But the first question is, What is the origin of these barbs, and how are they developed from the object we see in Fig. 2? Curiously enough, the key to this puzzle was unwittingly stumbled upon by Ruprecht in 1852. He noticed upon the fin-like expansion which extends between the body and the arms of the green fruit the parallel darker streaks marked *f* in Fig. 2; for he remarks that, upon dissection, he found imbedded in the softer, semitranslucent tissue, bundles of *braune Fasern*, and it is these brown fibers which, as we shall see, play an important part in one chapter of Phyllospadix life history.

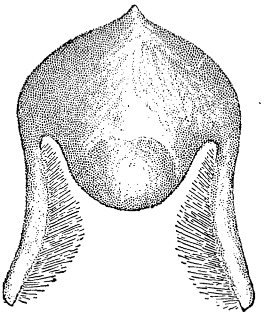

FIG. 3.— Fruit as found attached to Amphiroa.

In Fig. 4 is shown a diagrammatic section of the stage of fruit shown in Fig. 2, cut in the plane of the two arms. The pericarp is here so differentiated that we may distinguish, for convenience, two parts, — what we may call the exocarp, the soft, spongy outer portion; and the endocarp. The latter is thin or absent at the lower end of the seed, but it clasps the body of it as in a sling of tough, compact tissue, composed of elongated lignified cells. Further, this endocarp, prolonged downward, forms the axes of the arms; and, finally, it produces a great number of very long and thick-walled cells, which lie loosely imbedded in the softer substance of the "fin" (*f*). These "fibers" may be easily separated from one another, and from the enclosing exocarp, except at their lower ends, where they are conjoined with the endocarp of the arms. These slender lignified cells are the *Fasern* of Ruprecht, and now it is to be inquired how they are metamorphosed into the barbs of Fig. 3.

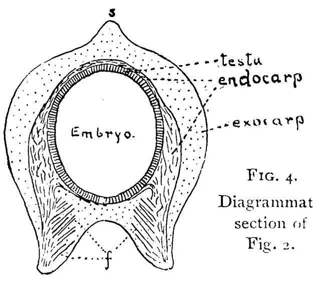

Fig. 4. Diagrammatic section of Fig. 2.

When the ripe fruit is ready to break loose from the spadix, its arms have grown longer and stiffer, as in Fig. 3, but are still, of course, enclosed in the exocarp. Now the fruit begins to drift about, — flung against the rocks, washed up on the beach, and sucked back again, bruised and scoured, in the swirling sand and pebbles of the undertow; and after a little of this rough-and-tumble existence the spongy exocarp begins to wear away, leaving exposed, in the arms and about the upper part of the seed, the hard endocarp, while about the base (*i.e.*, the lower middle part of Fig. 3) there is laid bare the smooth surface of the shell-like testa. But the important point is that the exocarp in which the barbs are imbedded is also got rid of. It easily flakes off and is washed away, and then, with a little more sand-scouring, the freed barbs, springing apart a little, stand out clean, like so many whalebones.

Now our "anchoring mechanism" is uncovered and ready for use. By this time, too, the seed may be ready to germinate, and, for the safe putting forth of leaves, a fixed abiding place is necessary. The seed must be anchored, and, the anchors being ready, the next requisite is a suitable anchoring ground.

Along our coast there are various species of coralline seaweeds (Corallina, Amphiroa) which abound wherever there are rocks between tide-lines. These algæ have slender, lime-impregnated stems, made flexible by being broken into short joints, and constricted between the joints like a string of coral beads; and they form an intricate, often turf-like, growth over the wave-washed rock.

We could not imagine a better opportunity for Phyllospadix in search of a lodging place; and it seems that Phyllospadix is, in fact, not slow to catch on, for experience showed that the more profitable way to collect Phyllospadix seed was to search at low tide, not in the eelgrass itself, but rather among the corallines covering some flat rock just inshore from the eelgrass beds.

When the fruit, hurried landward by a wave, blunders against a tip of Amphiroa, there is a fair chance that the stem will slip into the crotch of one of the arms. When once this has happened the wanderings of Phyllospadix are over. The many barbs unite to hold whatever is caught, and further knocking about by the waves only serves to wedge the alga more tightly into the grasp of the seed. The segmented structure of the Amphiroa prevents it from slipping through the grip of the arm, and so the seed is safely planted, as it were, in a tree-top. Frequently it even catches two branches of its host, one in either armpit, and so swings secure on two anchors.

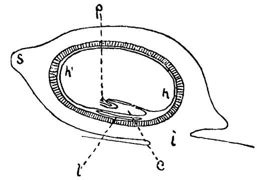

FIG. 5. — Diagram of dorsiventral median section of Fig. 2. *c*, cotyledon: *i*, insertion of pistil; *h*, *h'*, hypocotyl; *l*, folded edge of hypocotyl.

Time and seed are now ripe for germination. What next takes place will be better understood upon referring to Fig. 5. Here is a longitudinal, dorsiventral, median section of the immature fruit. The cavity of the seed is filled by the embryo, of which the bulk consists in the hypocotyl (*h*, *h'*). The cotyledon (*c*) is short, straight, and tubular, and serves merely as a sheath for the plumule (*p*). It lies upon the ventral side — as regards the pistil — of the hypocotyl, and points toward the base, *i.e.*, in the direction of the arms. The testa (*t*) is formed of a single layer of cells with thick, lignified cell walls, and thus, while it serves, like an arch of bricks, to protect the embryo from outside pressure, it is readily burst open by the swelling within of the hypocotyl.

Perhaps the exposure, and consequent partial drying of the seed, at low tide helps to crack the testa. At any rate, when germination begins the basal end (*h*) of the hypocotyl bursts through the testa and presses the broken edge of it back, leaving a clear passage for the cotyledon. The hypocotyl grows no farther than this, and eventually, when its store of substance has served to give the young plant a start, it dies away.

The cotyledon grows out little beyond the hypocotyl, and is quickly outstripped by the ensheathed plumule, which turns upward and shortly unfolds to the waves several grass-like leaves (Fig. 6). Henceforth it is these leaves only which grow upward; for, except for the slender peduncle which bears the inflorescence, the only stem of the mature Phyllospadix is a creeping rootstock, or rhizome.

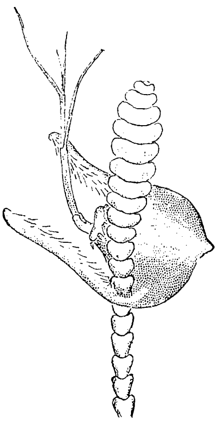

Fig. 6. — Seedling with first leaves.

Our seedling (Fig. 6) has now quite a start in life, and yet it has no root. Its leaves, meanwhile, whipped back and forth by the waves, are gradually beaten to shreds, and replaced by others. In this way several of the first leaves may have lived and died before any root appears. At last, when roots are put forth, there are two of them produced, not from the hypocotyl, as we might expect, but from the stem above the cotyledon (*r*, Fig. 7). That is to say, these are, in the technical sense, adventitious roots. When full grown the roots are about two centimeters long, stout, and unbranched. This first pair hang down, one on either side of the stem, and are soon followed by several more which grow out from the second internode.

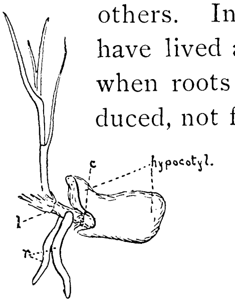

Fig. 7. — Young seedling with coats removed. *c*, insertion and remnant of cotyledon; *l*, second node with remnant of leaf; *r*, roots.

When the roots are several millimeters long they begin to produce, near their tips, a dense, woolly covering of root-hairs, and when a root comes in contact with any object, — be it the stem of the Amphiroa (Fig. 8), the rock beneath, or another root, — these rhizoidal hairs spread, as a closely adhering film of whitish fibers, over the surface touched, binding the root to it. The root-hairs assume fantastic shapes in order to conform with the irregularities of the rock. If a root has, by chance, entered the loose sand, it becomes enclosed in a compact cylinder of sand, bound together by the myriad of branching, interwoven hairs.

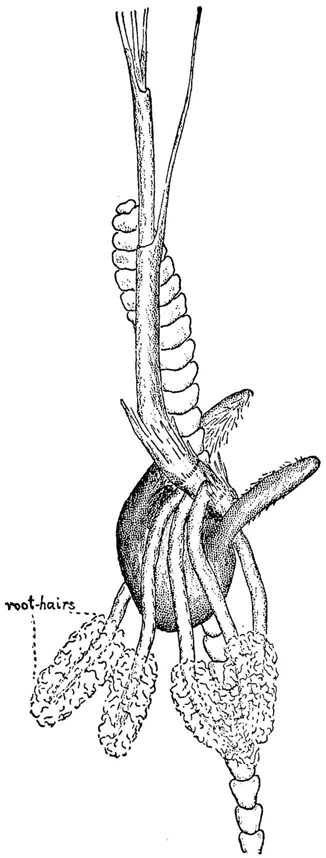

Fig. 8. — Seedling (older) with roots.

The plant has now taken a firm hold on life. Supposing that the start has been made aloft in the branches of the Amphiroa, the elongating stem now dips downward till it strikes the rock. Thenceforth it creeps along, taking, as it goes, a firm grip upon every inch. At each node it bears a leaf, and each of the short internodes produces, on one side a supra-axillary bud, and on the other what Professor Dudley[1] has aptly termed an "epaulette" of six or eight roots; alternating, so that, if one internode has its roots on the right side, the next will have roots on the left. Thus the stem, though in itself weak and brittle, keeps a close, broad grasp upon the rock, while the wiry leaves, buoyed by intercellular air-spaces, stream upward sometimes for a length of two meters. Before these leaves have been whipped to tatters by the waves, their place is supplied with new ones from the lateral buds.

When the rhizome has reached a length of, often, only one or two decimeters, it begins to die away behind. At the same time the lateral buds begin to push out for themselves, so that as the parent stem creeps on it leaves on either side of its trail a series of new rhizomes, starting out at right angles to the old one. In like manner this new generation of rhizomes branch and rebranch, growing over and upon one another, till, in a few years, the bowlders, as well as the bed-rock, are covered by a patch of eelgrass, — a thick mattress, which, as it lies in sinuous tangles at low tide, quite dissipates the force of a hammer, though swung with all the energy of an enthusiastic botanist, and so must, one would think, considerably lessen the effect of the forces which are ordinarily at work reducing the bowlders to pebbles and grinding down the rock itself.

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[1] *Cf.* Dudley, R. W., in *Zoe*, vol. iv, p. 381.

This brings us to the second phase of our subject, namely, the significance of such a plant as Phyllospadix to the geologist. What we wish to show is that under some conditions the effects of the plant in modifying the results of wave and current action are worthy of consideration.

Various geological authorities have commented upon the protection afforded to shore rocks by some marine plants, and upon the accumulation of detritus by others. Certainly no plant is better adapted to either of these functions than Phyllospadix. In the first place its manner of growth is exceptional, resulting, as it does, in the formation of a broad, continuous patch, instead of a scattering of individuals. Again, unlike the soft or rubbery fronds of the algæ, its leaves are strengthened by extremely tough bands of collenchyma fibers.

A moment ago we noticed how the eelgrass bed, the growth of which from a seedling we have sketched, covers the bowlders with a thick mattress which must prevent attrition between the loose stones and pebbles. At Bodega Bay may be seen such a bed, where, at low tide, one may stumble for rods along a bowlder-strewn shore without seeing the rock under foot, all being overlaid by the tangled mat of eelgrass. Now, it might be objected that the corrosive action of the acids excreted by root-hairs would offset the protection the plant might afford to the rock. But it is at once obvious that the root-hairs of Phyllospadix are, in this respect, unlike those of most plants. Their essential function is that of attachment, not nutrition, and, of course, if they should cut the ground from under their own feet, so to speak, by dissolving away the rock to which they ought to hold fast, they would be useless.

Suppose, now, that a wave-cut terrace, which is being widened by the inroads of the sea, and which is swept by a littoral current bearing the shore-drift along with it, becomes overspread by a growth of coralline algæ. Geike, in his *Text-Book of Geology*, speaks of the preservation of shore rocks by the overgrowth of these corallines ("calcareous nullipores"). These plants cover the substratum with a brittle, calcareous crust, which, though a considerable protection against the cutting of water-borne sand, is shattered by the blow of a pebble. This calcareous enameling retards, to some extent, the lowering of the terrace by the sand-bearing current. That is, while the terrace widens, the water above it may remain comparatively shallow. Moreover, many of these corallines, as Amphiroa and Corallina, produce, in addition to the calcareous crust, numerous erect, jointed fronds; and the latter, as we have seen, offer the best possible lodging place for Phyllospadix. Here, then, we have the conditions most favorable to Phyllospadix, — shallow, but not quiet, water, and corallines to anchor the seeds.

Gradually, if there is eelgrass within drifting distance, the terrace becomes dotted with green tufts, the tufts spread into patches, and ultimately the higher border of the terrace presents, at low tide, the appearance of a wind-laid hay-field, the "grass," one to two meters long, lying in prostrate tangles.

Now begins the accumulation of debris. Stones and pebbles being carried alongshore by the current, odds and ends of seaweeds, and all the multifarious small drift of the shore, are caught in the network of rhizomes and wiry leaves. The larger stones may themselves serve as footholds upon which the rhizomes climb higher and wave their leaves higher in the water. Every stone entangled serves to stop more pebbles and sand, and, as the mass continues to pile up, the rhizomes are at last buried deep under it; but as long as the tips of the leaves wave free the plant thrives. On almost any of our beaches there may be found between tide-lines tufts of slender leaves apparently growing in the sand, but in reality anchored to the rock a meter, perhaps, below.

The result of the accumulations, then, is that the water is made shallower, so that, though the pounding of the heavy seas upon the shore is lessened, the waves still race in over the shallows and carry up the smaller particles to deposit them on the beach. At the same time, even though the littoral drift be not held permanently by the eelgrass, yet the time required for it to pass the place, and hence its chance of contributing to the beach, is increased.

Shoaler and shoaler grows the water, the shore line advancing as a low beach, and finally, — the littoral current being deflected seaward and the wave deposition continuing, — the terrace that was is overlaid by a sand-flat.

That the long, hemp-like fibers of eelgrass lend coherence to the mass of sand and stones in which they are imbedded is attested by the fact that where, as above, we find a clump of eelgrass half-buried in the sand, the level of sand within the clump is often several inches above that of the surrounding beach.

In closing, and to recapitulate, it seems probable that the spreading over a terrace of such a plant as Phyllospadix must tend, first, to protect the rocks from erosion and attrition ; second, to help, by trapping the shore-drift, to raise the terrace so as to form a beach, or a sublittoral sand-flat ; and last, by binding together its materials, to render the foundation of the beach, once formed, more coherent and stable.

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